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Plant evolution: landmarks on the path to terrestrial life

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Summary

Photosynthetic eukaryotes thrive anywhere there is sunlight and water. But while such organisms are exceptionally diverse in form and function, only one phototrophic lineage succeeded in rising above its substrate: the land plants (embryophytes). Molecular phylogenetic data show that land plants evolved from streptophyte algae most closely related to extant Zygnematophyceae, and one of the principal aims of plant evolutionary biology is to uncover the key features of such algae that enabled this important transition. At the present time, however, mosaic and reductive evolution blur our picture of the closest algal ancestors of plants. Here we discuss recent progress and problems in inferring the biology of the algal progenitor of the terrestrial photosynthetic macrobiome.

I. The singularity of plant terrestrialization

Over the billion-plus yr evolutionary history of photosynthetic eukaryotes, a wide range of algae successfully established themselves on land. This includes members of the Chloroplastida (green algae), but there are also reports of terrestrial Rhodophyta (red algae) as well as complex plastid-bearing lineages such as diatoms (Hoffmann, 1989; Raven & Edwards, 2014), the survival of which appears to hinge on the formation of desiccation-tolerant resting cells (Souffreau *et al.*, 2013). Such algae possess various biochemical and (photo-)physiological adaptations that enabled this transition (see e.g. Holzinger & Karsten, 2013), and various lines of evidence suggest that they evolved a terrestrial lifestyle multiple times independently. Some of these lineages – including those that lichenize – might even have been on land long before land plants came to be (Raven & Edwards, 2014). Despite these independent adaptations – especially within the green lineage (Lewis & McCourt, 2004) – all of the terrestrial macroflora is derived from a single clade within the Streptophyta (Wickett *et al.*, 2014; Fig. 1). Simply put, land plants evolved once; the biological significance of this singularity is writ large across the surface of the globe.

Given that plants evolved from within streptophytes, there is considerable interest in trying to reconstruct early land plant evolution through the lens of streptophyte algae. Among the most fundamental questions in the field are: which specific lineage of streptophyte algae gave rise to the land plants; and what was it about the biology of this lineage that enabled its conquest of land? The answer to the first question is now in hand. The paraphyletic streptophyte algae can be divided into the lower-branching KCM-grade (Klebsormidiophyceae, Chlorokybophyceae and

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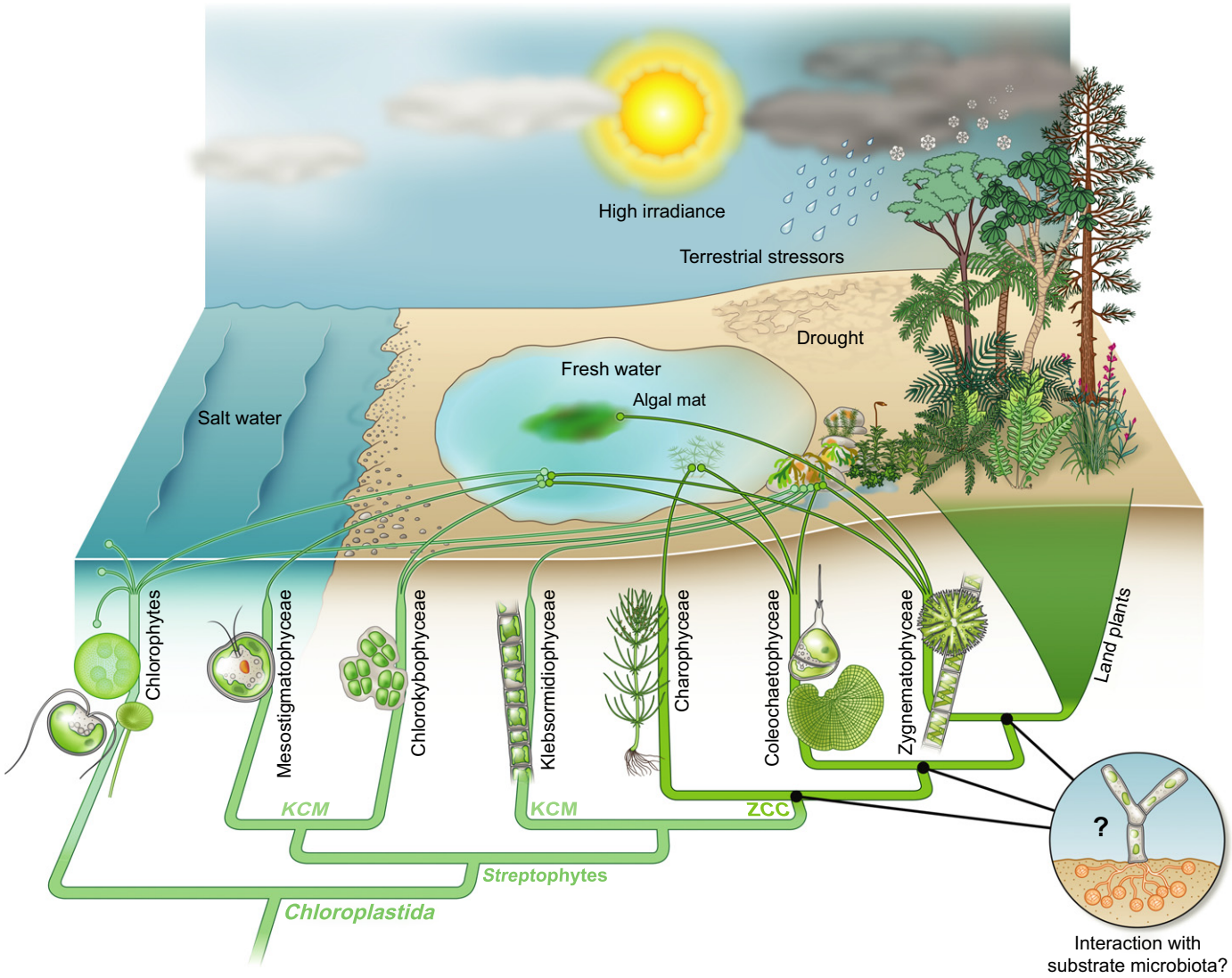

Fig. 1 Streptophyte terrestrialization and the colonization of terrestrial habitats by extant Chloroplastida. Approximately 1 billion yr ago, the green lineage (Chloroplastida) split into the chlorophytes and streptophytes. The streptophytes consist of the monophyletic embryophytes (land plants) and paraphyletic streptophyte algae; streptophyte algae can further be subdivided into the basal-branching Klebsormidiophyceae, Chlorokybophyceae, and Mesostigmatophyceae (KCM) grade and the higher-branching Zygnematophyceae, Coleochaetophyceae, and Charophyceae (ZCC) grade. Chlorophytes occur in a variety of marine, freshwater and terrestrial environments. Streptophyte algae are found in freshwater and terrestrial habitats, for example, in wet soil or on rock surfaces, down in the sediment of lakes and streams (Charophyceae) or on these as algal mats (Zygnematophyceae); some Coleochaetophycae even grow as epiphytes on Charophyceae. Note also that various extant chloroplastidial algae grow on land plants (e.g. on tree barks). While the ability to dwell in terrestrial habitats exists across the diversity of Chloroplastida, only the land plants dominate the macrobiome of the Earth's surface, unparalleled in their morphological and species richness. Inferring the traits of the algal ancestor of land plants – a group of organisms closely related to extant Zygnematophyceae – requires assessment of the biology of ZCC grade streptophyte algae. The emerging consensus is that it was an organism with branching filaments (or perhaps even pseudoparenchymatous growth) that interacted with beneficial (substrate) microbiota, probably including the ancestors of mycorrhizal fungi. The algal embryophyte progenitor probably also possessed a physiology that allowed it to cope with terrestrial stressors such as drought/desiccation, high ultraviolet and photosynthetic irradiance, and rapid temperature changes.

Mesostigmatophyceae) and the higher-branching ZCC-grade (Zygnematophyceae, Coleochaetophyceae, and Charophyceae; see Box 1, Fig. 1; also see de Vries *et al.*, 2016). For some time it seemed as though there had been a stepwise increase in organismal complexity, from a unicellular alga like extant *Mesostigma* (see Marin & Melkonian, 1999), through to simple filamentous forms such as *Klebsormidium* and *Zygnema*, on to pseudoparenchymatous apical cell-bearing *Coleochaete*, and, finally, to a complex multicellular organism like *Chara*, a stonewort with rhizoids and stem-like structures (Fig. 1). However, recent phylogenomic analyses show a sister relationship between land plants and the Zygnematophycae, an enigmatic group of unicellular and filamentous algae that live in a variety of freshwater and terrestrial environments (Wodniok *et al.*, 2011; Timme *et al.*, 2012; Ruhfel *et al.*, 2014; Wickett *et al.*,

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Box 1 Glossary

Chloroplastida – the monophyletic 'green' lineage consisting of the chlorophytes (green algae) and streptophytes.
Homoiohydry – a dehydration-avoidance mechanism based on active maintenance of water homeostasis – especially under water-limiting conditions; the predominant mechanism employed by vascular land plants to tolerate water limitations.
KCM grade – a paraphylum consisting of the basal-branching streptophyte algal clades Klebsormidiophyceae, Chlorokybophyceae, and Mesostigmatophyceae.
Phragmoplast – a scaffold of cytoskeletal components and vesicles that is formed during anaphase/telophase; a textbook characteristic of the land plant-type cell division.
Poikilohydry – passive equilibration of the cell's water status to that of the environment; can lead to desiccation under water-limiting conditions, which is tolerated by only some photosynthetic eukaryotes such as certain algae (including some streptophyte algae), lichens, mosses and very few vascular plants.
Preprophase band – an actin and tubulin scaffold that forms during the end of the G2 phase of Zygnematophyceae and land plants (for a comprehensive discussion, see Buschmann & Zachgo, 2016).
Primary plasmodesmata – cell wall channels that are formed during cell division (as opposed to secondary plasmodesmata, which are formed independently of cell division).
Sporopollenin – the highly robust material that coats spores of algae, embryophytes, and fungi. It consists of a complex mixture of biopolymers, including (but not limited to) phenolic compounds and fatty acids; best known as the robust coating of pollen.
Streptophytes – a monophyletic group uniting the streptophyte algae (also known as charophytes) and land plants.
ZCC grade – a paraphylum of the higher-branching streptophyte algal clades Zygnematophyceae, Coleochaetophyceae, and Charophyceae, which are sister to land plants.

2014). Given that the Zygnematophyceae have the least complex bodyplan of all higher-branching streptophyte algae (i.e. the ZCC grade), this comes as something of a surprise. As we shall see, inferring the evolution of traits along the trajectory of streptophyte evolution has proved challenging.

The second question is much more difficult. Evolution is a dynamic process; extant organisms are snapshots in time and provide only static, and often misleading, information about how they came to be. In order to infer the features of streptophyte algae that were relevant to the conquest of land, one needs not only to consider present-day Zygnematophycae, but also to look at their ancestry. To identify informative features, it is crucial to consider what plant terrestrialization actually means. In thinking about the success of land plants, obviously adaptive traits such as the presence of desiccation-tolerant seeds, vascular tissues (which conduct water and provide stability), and gas-exchanging stomata quickly come to mind. These are certainly essential features of the (homoiohydric; see Box 1) plant cormus – the true plant body – and > 400 million-yr-old fossils exhibiting many of these properties have been found (reviewed by Gensel, 2008). However, the cormus arose *within* land plants; the aforementioned features are hence the subject of the evolution of plants on land. Towards a complete understanding of land plant evolution we must also consider what came about *before* such features arose. The question is more than what the first vegetative body looked like. It is a physiological question about how the organisms that eventually gave rise to land plants overcame the challenges associated with dry land (reviewed by Delwiche & Cooper, 2015). Cellular physiology and bodyplan evolution are in fact two sides of the same coin: a more complex bodyplan allows for cellular differentiation, which later proved to be essential for the evolution of specific tissues (e.g. water-conducing vasculature) and land plant homoiohydry. But the algal ancestor of embryophytes was a poikilohydric organism – just like any other (extant) terrestrial microalga, which can also grow in diverse and challenging environments.

The algal progenitor of embryophytes did more than just dwell in a terrestrial habitat such as moist soil or rock. It conquered all parts *terra firma*, presumably in a stepwise fashion. What physiological properties allowed the first land plants to thrive such that the complex adaptations so familiar to plant biologists could evolve? Here we discuss some of the concepts and challenges associated with inferring early steps in land plant evolution.

II. Adaptation vs exaptation – what shaped the land plant toolkit?

Dry land is a high-stress environment. This is especially true for photosynthetic organisms, which first evolved in aquatic habitats. On land, light is not filtered by water (Maberly, 2014; Fig. 1); high irradiance is thus an inescapable threat, increasing the risk of photooxidative and UV damage (see, e.g., Karsten & Holzinger, 2014). Furthermore, stressors such as drought and severe cold (including freezing) directly impact photosynthetic performance and are among the key inducers of plastid-nucleus communication (for review see Chan *et al.*, 2016; see Rippin *et al.*, 2017 for a recent overview of the pronounced impact of desiccation stress on gene expression in streptophyte algal photosynthesis). But while modern-day plastids are hard-wired into the stress response signaling pathways of the cell (see also de Vries *et al.*, 2016), various other plastid-independent features of the algal cell are thought to have aided the process of terrestrialization.

Foremost among such properties is the evolution of a sturdy cell wall, undoubtedly a useful trait on land. Certain cell wall reinforcements and modifications are key during dehydration stress (Kroken *et al.*, 1996; Holzinger & Karsten, 2013; Herburger & Holzinger, 2015). They can also provide stability and allow for the development of asymmetric structures (see Harholt *et al.*, 2016). Streptophyte algae – especially those of the ZCC grade – are noteworthy in containing cell walls with lignin-like components (Delwiche *et al.*, 1989), a feature that resembles land plants. This is underscored by the presence of sporopollenin (see Box 1) in zygotes of Zygnematophyceae (de Vries *et al.*, 1983), Coleochaetophyceae (Delwiche *et al.*, 1989), and Charophyceae (Blackmore & Barnes, 1987). Furthermore, the cell wall polymer profiles of ZCC grade streptophyte algae match those of land plants more than do those of the KCM grade (Sørensen *et al.*, 2011). Streptophyte algae also appear to possess the makings of a phenylpropanoid pathway (de Vries *et al.*, 2017), which is important given that phenolic

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compounds are thought to shield against UV irradiance (Popper *et al.*, 2011). It also serves as a foundation for the evolution of land plant homoiohydry, which is aided by phenylpropanoid derivatives.

Clearly the streptophyte ancestors of land plants were forced to deal with stress. The elaborate stress signaling pathways of extant land plants (see e.g. Song *et al.*, 2016 or Scheres & van der Putten, 2017) speak to turbulent times during their early evolution. The signaling pathways of land plants often depend on phytohormones. Phytohormone-mediated signaling (homologous to that of land plants) has been detected in various streptophyte algae (Delaux *et al.*, 2012; Hori *et al.*, 2014; Ju *et al.*, 2015; Van de Poel *et al.*, 2016; Ohtaka *et al.*, 2017) and polar transport of the phytohormone auxin has been shown for both *Klebsormidium* and *Chara* (Boot *et al.*, 2012; Ohtaka *et al.*, 2017). Furthermore, comparative genomic investigations reveal that the land plant common ancestor possessed a complex gene expression regulatory network that utilized 47 out of the 48 transcription factor families known from modern-day land plants (Catarino *et al.*, 2016). This has important implications on various levels, including the evolution of morphological complexity (Lang *et al.*, 2010; Breuninger *et al.*, 2016). All things considered, a substantial fraction of the (molecular) physiological tools that land plants use when coping with the challenges of terrestrial life can be seen in streptophyte algae.

But while streptophyte algae bear features that aid a terrestrial lifestyle, some of these algae dwell on land and some do not (Fig. 1). For example, *Coleochaete*, with its sturdy cell wall and complex bodyplan, tolerates desiccation (Graham *et al.*, 2012) but is not in fact terrestrial – it grows in freshwater habitats (Fig. 1). Similarly, Herburger & Holzinger (2015) found that while two species of the KCM streptophyte algal genus *Klebsormidium* reinforced their cell walls with callose upon desiccation stress, two ZCC algal species of the genus *Zygnema* – which are more closely related to land plants – did not. This is despite the fact that the cell wall polymer profile of ZCC streptophytes is more similar to land plants than that of the early-diverging KCM algae (Sørensen *et al.*, 2011). Further, based on nonphotochemical quenching analyses, two *Klebsormidium* spp. showed higher tolerance towards high light than did a *Zygnema* sp. (Pierangelini *et al.*, 2017). Overall, these data paint a very blurred picture of the distribution of physiological properties conducive to living on land across streptophyte algae. Indeed, terrestrial algae are found scattered across the diversity of the entire green lineage (Lewis & McCourt, 2004; Fig. 1). This raises the following question: in which environment and, hence, under which selective forces did the key features aiding the conquest of land evolve?

If such features arose whilst streptophyte algae resided in a freshwater environment, then they were exaptations (also known as pre-adaptations) (see Becker & Marin, 2009); they evolved for some purpose in water and only later proved advantageous on land. By contrast, such features could represent true adaptations, that is, they evolved under selection pressures associated with terrestrial life. The latter scenario was recently endorsed by Harholt *et al.* (2016), who stated that 'plants were terrestrial from the beginning'. Both viewpoints have strengths and weaknesses, but it is difficult to know how to weigh up their relative contributions. Indeed, the specific traits of extant organisms can often be interpreted in favor of one or the other depending on one's point of view. Consider, for example, the specific cell wall properties that streptophyte algae share with land plants. They are clearly conducive to a terrestrial lifestyle but are nevertheless also found in aquatic streptophyte algae. Such characters can reasonably be interpreted as ancient terrestrial adaptations, but if so, then one must also consider why they also exist in aquatic lineages. The forces contributing to the evolution of any given trait were undoubtedly complex and context-dependent; any given trait must be considered in isolation, and what is an adaptation in one environment may be an exaptation in another. In a sense, the mystery of early land plant evolution ultimately boils down to the question of why it was a singularity. It seems unlikely that it was just one feature – either an exaptation or adaptation – that aided terrestrialization. The successful land (plant) conqueror, i.e. the ancestral embryophyte, must surely have had all the equipment needed to overcome the challenges faced on *terra firma*, a toolbox full of both adaptations and exaptations. The genome sequences of extant plants provide a window through which to infer its contents.

III. Trait mosaicism in (higher-branching) streptophyte algae

Evolutionary biologists are drawn to singularities. Such events often represent major leaps and lack clear intermediates. The origin of land plants has long been considered a case in point. But the more we look at large-scale sequencing data from streptophyte algae, the more we find genes once considered land plant-specific (e.g. Hori *et al.*, 2014; Delaux *et al.*, 2015; Ju *et al.*, 2015; de Vries *et al.*, 2017). Furthermore, the use of such data for phylogenomics has enhanced our understanding of the closest algal relatives of land plants (see Wickett *et al.*, 2014). But phylogenomics has also left us puzzled. As noted earlier, the Zygnematophyceae, morphologically the least complex of the higher-branching streptophyte algae, branch as the closest algal relatives to land plants (Fig. 1). This branching order underscores the problem of inferring the character set of land plants' algal ancestor.

Of course, since they last diverged from a common ancestor, each lineage charted its own evolutionary path. In the case of the Zygnematophyceae – and based on the complex bodyplan that the common ancestor of Charophyceae and Coleochaetophyceae probably had – this probably involved reductive evolution. Yet caution is advisable. Zygnematophyceae are sometimes considered unbranched, but they do branch and form holdfasts (see, e.g., Stancheva *et al.*, 2014; and Delwiche & Cooper, 2015). Hence, the common ancestor of all ZCC grade algae probably featured at least a branching bodyplan (Fig. 1, insert; see also Delwiche & Cooper, 2015), from where the evolution of pseudoparenchymatous development, as observed in Coleochaetophyceae, and the complex bodyplans of Charophyceae is just another step. Going hand in hand with this was the evolution of features such as meristems (Charophyceae and Coleochaetophyceae; see Graham *et al.*, 2000), gravitropism (Charophyceae; see Hodick, 1994), and a more refined cellular localization of growth-mediating enzymes such as cell wall modifiers (Herburger *et al.*, 2017).

Delwiche (2016) recently emphasized the fact that each extant streptophyte lineage appears to have its own set of derived and

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ancestral features. The only way to reassemble the ancestral suite of features is thus a comparative approach. But our datasets will never be complete. For example, within the Charophyceae, extant taxa represent a small fraction of the diversity that existed in Devonian times (see Feist *et al.*, 2005), which hampers efforts to assemble a complete trait catalogue. How can we then decide whether a given trait is truly ancestral and not the result of convergent evolution (i.e. a homoplasy)? The most parsimonious approach is to assume that if a trait is shared by multiple lineages, it must have arisen in their last common ancestor. This is not unreasonable, but it can result in an additive effect whereby we must infer an ever more complex common ancestor and, in the case of patchily distributed traits, ever more independent losses.

Consider cell division and the concomitant formation of primary plasmodesmata (intercellular junctions). Primary plasmodesmata are found in Charophyceae and land plants (Cook *et al.*, 1997; see also Brunkard & Zambryski, 2016); the combination of a preprophase band (see Box 1) and phragmoplast formation during cell division is limited to land plants and some Zygnematophyceae (Buschmann & Zachgo, 2016). Hence, it is only the ZCC grade as a whole (in this example Zygnematophyceae and Charophyceae) that exhibits land plant cell division traits that combine the formation of primary plasmodesmata, a preprophase band and a phragmoplast. Given such complexity, a more nuanced approach to inferring trait evolution is desirable, one that includes consideration of the molecular and biochemical underpinnings of such traits. Once a critical threshold of genes and regulatory circuits has been reached, the 'evolvability' of the characters they can give rise to increases. This can lead to the illusion of independent origins of certain characters, when they are in fact the product of a similar molecular chassis. Defining the common ZCC feature list with the goal of understanding the algal ancestor of land plants is thus not just about specific genes, but also about pathways and genetic potential.

A good example of latent genetic potential is the realization that streptophyte algae possess a near-complete set of genes underlying the so-called 'symbiosis signaling module', which in plants plays a key role in establishing symbiotic interactions with mycorrhizal fungi (Delaux *et al.*, 2015; see also Box 2). That said, Delaux *et al.* (2015) also found that downstream genes, such as those mediating root infection and cell-specific differentiation, are only found among land plants – probably the result of adaptive coevolution. This example illustrates how a complex trait (i.e. root–fungal symbiosis) can evolve from a core set of genes.

Box 2 Early land plants, beneficial substrate microbiota and the 'symbiosis signaling module'

Symbiotic interactions with fungal partners are thought to have been essential for the earliest land plants. Such interactions allowed for improved uptake of nutrients from the substrate and, hence, for its conquest (Field *et al.*, 2015). Fossil evidence underscores the presence of mycorrhizal-like structures in > 400 million-yr-old plants (Strullu-Derrien *et al.*, 2014) and relevant fungal taxa during the period when land plants evolved (Redecker *et al.*, 2000). Symbiotic interaction with mycorrhiza probably represents an ancestral feature of embryophytes (Selosse *et al.*, 2015). Furthermore, the pathway required for establishing associations with (arbuscular) mycorrhiza is found among all embryophytes (Delaux *et al.*, 2013) and streptophyte algae (Delaux *et al.*, 2015). As this pathway was later coopted for other 'classical' soil microbiota–plant symbioses, such as the root nodules (Parniske, 2008), it is considered to be the plant's 'symbiosis signaling module'. Significantly, this module is present in streptophyte algae (Delaux *et al.*, 2015). To what degree it operates in extant streptophytes in nature is unclear, but experiments have shown that in *Closterium* (Zygnematophyceae), a calcium- and calmodulin-dependent protein kinase (CCaMK) can rescue mycorrhiza formation-impaired *Medicago* mutant plants (*ccamk-1*) (Delaux *et al.*, 2015). Further, a comparative study of Coleochaetophyceae and liverworts showed that their microbiomes included potentially beneficial organisms such as nitrogen fixers (Knack *et al.*, 2015). A symbiotic perspective on early land plant evolution is in line with the notion that the earliest plant communities might have existed as 'cryptogamic covers' (see Edwards & Kenrick, 2015), which are community assemblies consisting of algae, cyanobacteria, fungi, lichens, and – in modern times – bryophytes. Hence, extant streptophyte algal–microbe interactions might mirror those occurring in the earliest land plant communities.

IV. Conclusions: a streptophyte algal perspective on land plant trait evolution

Traits that are hard-wired into the biology of land plants and are also found in streptophyte algae probably evolved in the latter. This includes the stress signaling components discussed earlier. Nevertheless, the complexity of such traits has increased considerably, in both streptophyte algae and land plants. Comparative studies of streptophyte algae can help to disentangle genetic potential and actual function, and, more generally, the role of chance and necessity in early plant evolution. Whether gene products work the same way today as they did in a common ancestor that lived many hundreds of millions of yr ago is often impossible to tell. But elucidating the functional and genetic potential of extant (ZCC) streptophyte algae as a whole will no doubt help us to understand plant terrestrialization. This will require extensive wet laboratory work with the right experimental tools and resources. In that vein, a streptophyte algal genome has already been sequenced (*Klebsormidium nitens*; Hori *et al.*, 2014) and several more are under way (Rensing, 2017). Transformation protocols are also being developed (Abe *et al.*, 2011; Vannerum *et al.*, 2011; Sørensen *et al.*, 2014). Streptophyte algae are thus gradually emerging as useful model systems (Chang *et al.*, 2016) with which to test hypotheses about the genetic underpinnings of land plant evolution. If the past decade is any indication, the next 10 years should be full of surprises.

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